

THE GENUS GENTIANOPSIS (GENTIANACEAE): TRANSFERS AND PHYTOGEOGRAPHIC COMMENTS

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I. THE GENUS GENTIANOPSIS.

The large genus *Gentiana* has long since been recognized as a very heterogeneous assemblage of morphologically diverse groups, so diverse that until recently no one has attempted in a rigorous way to delimit its more natural components. Rork (1949) and Löve (1953) pointed not only to the morphological diversity, but showed how extensive is the variation in chromosome number. Gillett (1957), in a careful and well illustrated monograph, removed from the North American *Gentianae* all taxa of *Gentianella*, a segregate genus long recognized by some European workers. *Gentianella*, *sensu stricto*, including *Gentianella campestris*, *G. germanica*, *G. quinquefolia*, *G. acuta*, and their allies, is certainly a very natural genus. However, Gillett's inclusion within his *Gentianella* of the celebrated and beautiful Fringed Gentians (as subgenus *Eublephis*) still leaves the botanist with an unnatural genus, for not only in floral characters and general aspect, but also in many other ways, such as their angular papillose seeds and the distribution of the ovules on the placentae, the Fringed Gentians form a natural and distinctive taxon easily distinguished from *Gentianella*. The segregated *Gentianopsis* thus gains a meaningful phylogeography and taxonomic integrity that would be lost within either *Gentiana* or *Gentianella*.

A recent clear segregation of the Fringed Gentians was carried out by Ma (1951), who established for the Asiatic and for some of the New World Fringed Gentians the genus *Gentianopsis*, giving full reasons in a short but clear English discussion (pp. 16-19). In his beautiful study of Japanese Gentianaceae, Toyokuni (1963) upheld Ma's genus, discussed its synonymy, and placed it in perspective to the rest of the Eastern Asiatic genera. Ma evidently intended to include all Fringed Gentians, but probably due to lack of available literature and specimens made transfers of only a few of the American taxa. The present study completes the transfers of these.

The generic characters of *Gentianopsis* on which it was established include, to quote Ma (1951:17):

1. its large and somewhat flattened ellipsoidal flower bud,
2. two dissimilar pairs of calyx lobes which are distichously imbricate in aestivation,
3. four triangular, ciliated intracalyx membranes at the base of and alternate with calyx lobes,

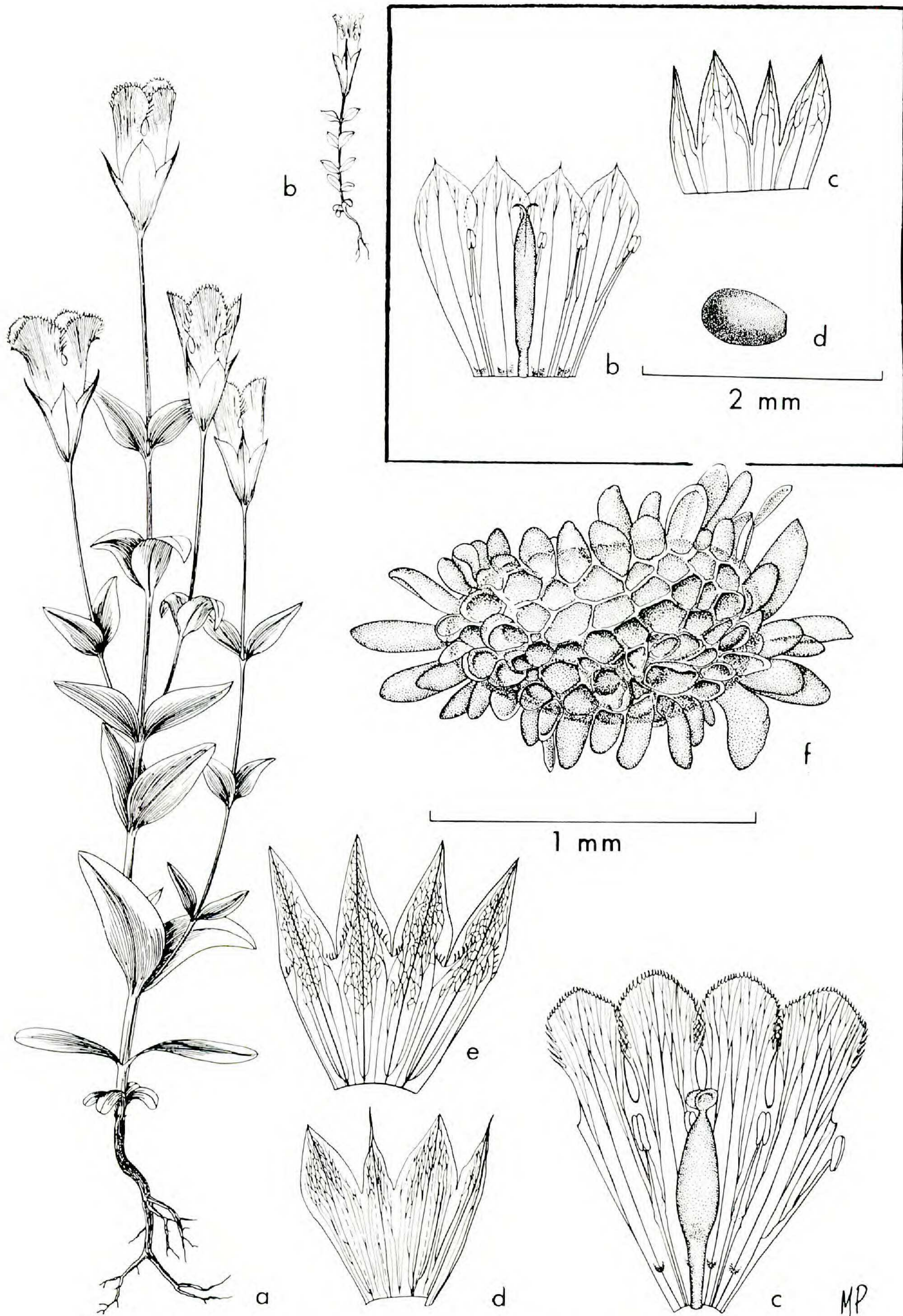


Fig. 1. *Gentianopsis crinita* and (insert) *Gentianella propinqua*, rearranged from Gillett (1963), with permission.

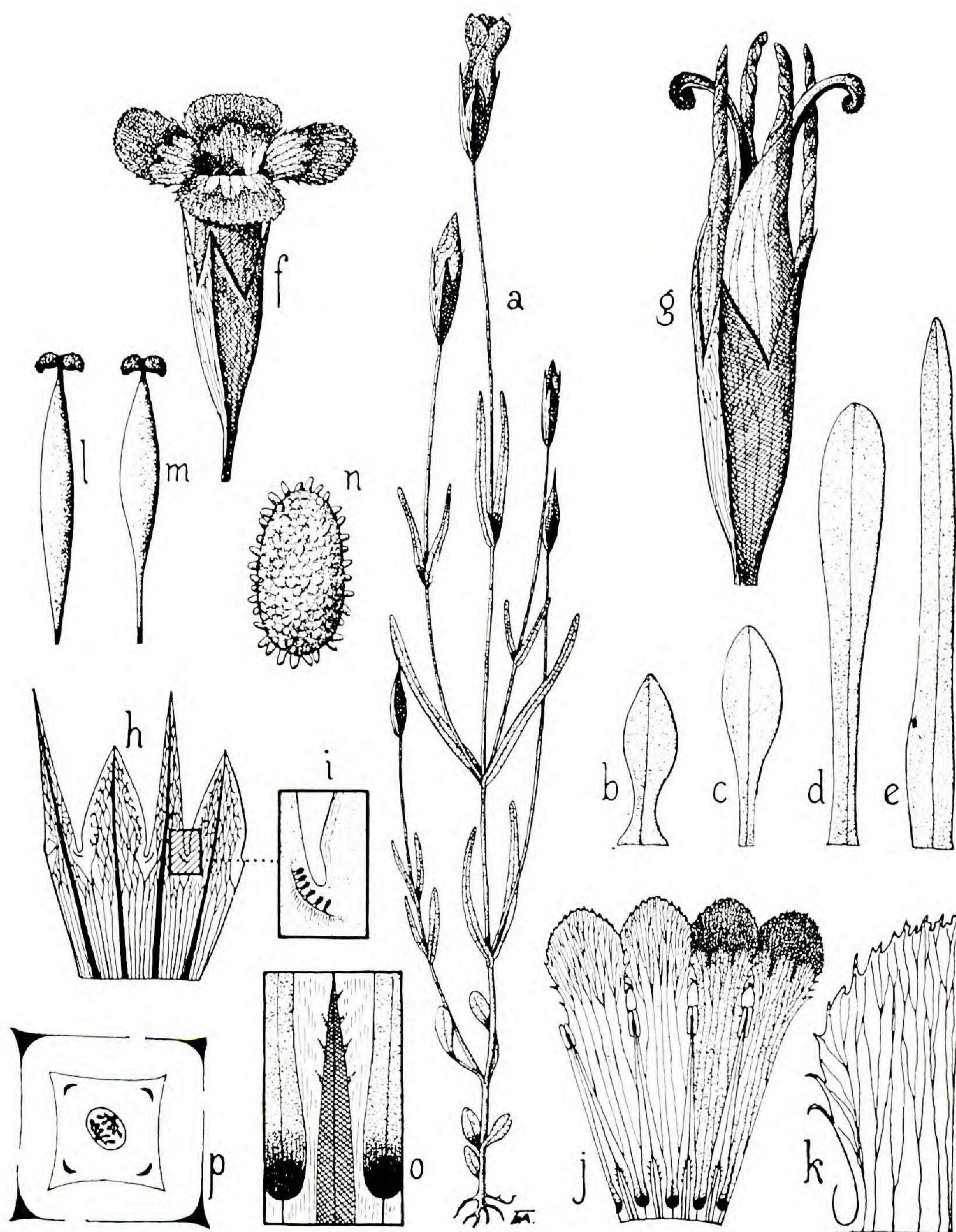
4. distinct gynophore, and
5. enlarged stigma (Fig. 2)

To these one might add:

6. the pronouncedly papillose angular seeds (Fig. 1),
7. the distinctive placement of the ovules, covering nearly the entire surface of the ovary wall,
8. the 4-merous flowers, and
9. the frequently fringed or toothed corolla-lobes.

All but one of these attributes apply well to the American taxa listed below, as can also be seen from the beautiful illustrations in Gillett (1963). The only character which does not hold uniformly is number 2, the dissimilarity in length of the calyx lobes, for while there is a tendency for unequal sepals, in many species the lobes are quite equal, as in *G. simplex*, *G. barbellata* and *G. raupii*. Lindsey (1940) showed that Sect. *Crossopetalum* (= *Gentianopsis*) has a markedly different floral anatomy from all other groups in *Gentiana*, *sensu lato*. Some of these characteristics are mentioned by Ma (1951) who contrasts them with those of *Gentianella*, *sensu stricto*, mentioning the distinctive vascularization of the calyx (eight bundles, four dorsal and four fused ventral, rather than 3 unfused ones in each lobe as in *Gentianella*), of the corolla (5 bundles in each lobe rather than 3, but with the laterals branched), and of the ovary (6 bundles rather than 4 main bundles). Two plates (our figs. 1 and 2) are here reproduced to illustrate the generic characters of *Gentianopsis*. *Gentianopsis* Ma is based on *Crossopetalum* Roth (1827), a generic name which cannot be used since it has a much earlier homonym in the *Celastraceae*. *Anthopogon* Necker (Elem. 2:12. 1790), used by Rydberg and others for this group, likewise is generally considered a *nomen invalidum*, for the components of Necker's "species," which correspond to our genera, are very inadequately described and mostly not indentifiable (cf. Gillett 1957:202). Furthermore, *Anthopogon* Nutt. 1818, a validly published generic synonym of the grass genus *Gymnopogon* Beauv., makes Rafinesque's validation of the *Gentian* genus, i.e. *Anthopogon* Necker ex Raf., a later, generic homonym.

Löve (1953) suggests on cytotaxonomical grounds that *G. crinita* and *G. procera* with 78 chromosomes (base number 13) should perhaps be placed in a different genus from *G. detonsa* and *G. ciliata* with 44 chromosomes (base number 11). It would seem, however, that the relatively small morphological differences are at most of infrageneric rather than generic magnitude, and that, considering how few of the *Gentianopsis* taxa are known cytotaxonomically and how many different chromosome numbers appear in *Gentiana*, *sensu stricto*, such a course would be at least premature. Incidentally, Toyokuni (1963: 148-9), who leaves *G. crinita* and *G. procera* in *Gentiana*, places *G. cruciata* and *G. phlogifolia* into *Gentianopsis*, though fortunately just in a list and without formal transfers. Both of these species belong to *Gentiana* Sect.



Gentiana Victorinii. — (a) Plante entière ($\times 0.6$). — (b, c, d) Feuilles de la base ($\times 1$). — (e) Feuille normale ($\times 1$). — (f) Fleur à l'anthèse ($\times 1$). — (g) Fruit à la déhiscence ($\times 1.25$). — (h) Calice, face ventrale ($\times 1.25$). — (i) Détail du précédent. — (j) Corolle et androcée ($\times 1$). — (k) Nervation d'un lobe du calice. — (l) Pistil d'une plante vivante ($\times 1$). — (m) Le même après dessiccation. Le style et le stipe sont en noir. — (n) Graine ($\times 25$). — (o) Base de l'étamine et nectaires. On voit par transparence la zone de concrescence du filet et de la corolle, et les poils cachés par les ailes. — (p) Coupe schématique de la fleur au-dessus du point de concrescence des sépales.

Aptera (Rork 1949), a group rather closely related to Sect. *Pneumonanthe* which includes the American "Bottle Gentians." *Gentiana cruciata*, despite its 4-merous flowers, is in no way related to *Gentianopsis*.

SYSTEMATIC LIST OF SPECIES AND INFRASPECIFIC TAXA

GENTIANOPSIS Ma, in Acta Phytotax. Sinica. 1:7. 1951; Satake, Bull. Chichibu Mus. Nat. Hist. 6:3. 1955; Toyokuni, Jour. Faculty Sci. Hokkaido Univ. Ser. V, Botany VII:198-202. 1963. (Type: *Gentiana barbata* Froel.).

GENTIANA L. Sp. Pl., ed. 1, 227. 1753, *pro parte*; Gen. Pl. ed. 5, 107. 1754, *pro parte*.

ANTHOPOGON Necker *ex* Raf., Fl. Tellur. 3:25. 1837, *pro parte*; *Gentiana* subgenus *Anthopogon* (Necker *ex* Raf.) Toyokuni, Hokuriku Jour. Bot. 6:33. 1957, *pro syn.*, *non* *Anthopogon* Nutt. Gen. North Am. Plants 1:181. 1818. = *Gymnopogon* Beauv. in Gramineae.

GENTIANELLA Moench, Meth. Pl. 482. 1794, *emend.*, Schustler, in Vestn. 1 Sjezdu Cesk. Bot. v Praze, 34. 1923, *pro parte*; Gillett, Ann. Mo. Bot. Gard. 44:208, 1957, *quoad* subgenus *Eublephis*.

GENTIANA **** CROSSOPETALAE Froel., Gent. Diss. 109. 1796.

CROSSOPETALUM Roth, Enum. Pl. Phaen. Germ. 1:516. 1827, *non* *Crossopetalum* P.Br. Hist. Jamaic. 145. 1756 (*Crossopetalon* Adans. Fam. ii. 1763) = *Myginda* L. in Celastraceae (*Fide* Index Kew.).

GENTIANA subg. EUBLEPHIS Raf., Med. Fl. 1:208. 1828; *Gentianella* subg. *Eublephis* (Raf.) Gillett, Ann. Mo. Bot. Garden 44:210. 1957.

GENTIANA subg. GENTIANOPSIS (Ma) Toyokuni, Hokuriku Jour. Bot. 6:33. 1957; *Gentiana* sect. *Gentianopsis* (Ma) Satake, Natur. Sci. Mus. Tokyo 24:141. 1957.

1. GENTIANOPSIS BARBATA (Froel.) Ma, Acta Phytotax. Sinica 1:8. 1951.

Gentiana barbata Froel. Gent. Diss. 114. 1796.

2. GENTIANOPSIS BARBATA (Froel.) Ma, var. SINENSIS Ma, *loc. cit.* 1:9. 1951.

3. GENTIANOPSIS GRANDIS (H. Smith) Ma, *loc. cit.* 1:9. 1951.

Gentiana grandis H. Smith, in Sitzungsanz. Ak. Wiss. Wien 63: 100. 1926.

4. GENTIANOPSIS SCABROMARGINATA (H. Smith) Ma, *loc. cit.* 1:10. 1951.

Gentianella scabromarginata H. Smith, in Hand. Mazz., Symb. Sin. 7:980. 1936, *nom. nud. in obs.*

Gentiana detonsa var. *ovato-deltoides* Burkill, Jour. Asiat. Soc. Bengal, n. ser., 2:319; Ling, in Fl. Ill. Nord. Chine 2:23, pl. 7. 1933.

5. GENTIANOPSIS PALUDOSA (Munro) Ma, *loc. cit.* 1:11. 1951.

Gentiana detonsa var. *paludosa* Hook. f., Hook. Ic. pl. 9: tab. 857. 1852.

Gentiana paludosa Munro MS. *ex* Hook. f. *loc. cit. pro syn.*

Fig. 2 (opposite). *Gentiana victorinii* (i.e. *Gentianopsis procera*, a segregate population from Quebec). From Rousseau (1932), with permission.

6. GENTIANOPSIS NANA (Ling) Ma, *loc. cit.* 1:12. 1951.
Gentiana detonsa var. *nana* Ling, Fl. Ill. Nord Chine 2:23, pl. 7. 1933.
7. GENTIANOPSIS LONGISTYLA Ma, *loc. cit.* 1:12. 1951.
8. GENTIANOPSIS LUTEA (Burkill) Ma, *loc. cit.* 1:13. 1951.
Gentiana detonsa var. *lutea* Burkill, Jour. Asiat. Soc. Bengal, n. ser., 2:319. 1906.
9. GENTIANOPSIS CONTORTA (Royle) Ma, *loc. cit.* 1:14. 1951.
Gentiana contorta Royle, Ill. Bot. Himalaya 278, t. 68, fig. 3. 1839.
10. GENTIANOPSIS CONTORTA var. WUI Ma, *loc. cit.* 1:15. 1951.
11. GENTIANOPSIS YABEI (Takeda & Hara) Ma, *loc. cit.* 1:19. 1951.
Gentiana yabei Takeda & Hara, Jour. Jap. Bot. 13:600, f. 45. 1937.
12. GENTIANOPSIS CILIATA (L.) Ma, *loc. cit.* 1:19. 1951.
Gentiana ciliata L. Sp. Pl. ed. 1. 231. 1753, exclusive of specimens from Canada.
13. GENTIANOPSIS DETONSA (Rottb.) Ma, *loc. cit.* 1:9. 1951.
Gentiana detonsa Rottb. Kiob. Selsk. Skr. (Acta Hafn.) 10:435. 1770.
Gentianella detonsa (Rottb.) G. Don, ssp. *yukonensis* Gillett, Ann. Missouri Bot. Gard. 44:215. 1957.
14. GENTIANOPSIS **nesophila** (Holm) Iltis, comb. nov.
Gentiana nesophila Holm, in Ottawa Naturalist 15:11. 1901.
15. GENTIANOPSIS **raupii** (Porsild) Iltis, comb. nov.
Gentiana Raupii Porsild, Sargentia 4:60. 1943.
16. GENTIANOPSIS **thermalis** (O. Ktz.) Iltis, comb. nov.
Gentiana thermalis O. Ktz. Rev. Gen. 2:427. 1891.
Gentiana elegans A. Nelson, in Bull. Torr. Bot. Club 33:148. 1898.
Gentianopsis elegans (A. Nelson) Ma, *loc. cit.* 1:19. 1951.

While Harrington (1954), for example, accepts *G. thermalis*, Gillett (1957) considers *G. elegans* Nelson the valid name, because a) "it is more widely known," b) "Nelson's specimen is of fine quality and is distributed among at least three herbaria and probably more" and c) "Kuntze's specimen has not been found."

Kuntze's description (1891:427), 10 full lines of print, is detailed and gives exact locality data, viz., "At the hot springs of the Geyser region of the United States Yellowstone National Park." Around these hot springs, which give this species its specific name, *G. thermalis* (= *G. elegans*), the only fringed gentian in the area, is exceedingly common, and forms at times a magnificent solid purple-blue border. In fact, it is so common that

"in 1926 the Fringed Gentian was chosen as the [Yellowstone National] park flower. It was an excellent choice, not only because it is considered one of the most beautiful of all the park flowers, but because it blooms throughout the entire tourist season. It is found

blooming at the beginning of the tourist season in June on the warm earth of the geyser basins, and it is still in bloom on some of the more protected places in the park when the last tourists leave in late September." (McDougall and Baggle 1936:100).

The original description does indeed suggest that "*G. thermalis* Kuntze [is] based on depauperate specimens" (Rydberg 1906), plants of which, Kuntze observed, he was "unfortunately able to collect only very few." His description reports flowers with greatly foreshortened peduncles and plants with low stunted growth, much smaller than is normally the case. Small wonder! For Otto Kuntze visited Yellowstone National Park probably in early (or mid?) October ["23/IX-18/X. Side trip by wagon later by horse through Idaho to Virginia City and Yellowstone Park (geyser region); Madison River Valley"—Translated from Kuntze, 1891, vol. I:XI] What a very late collection date, when heavy snows often fall in the region! This would easily explain the rarity of the species, as well as the low growth form, for even occasional mid-season plants are many-stemmed and seemingly acaulescent [e.g. *Denniston* Aug. 7, 1929 (WIS!); *Cowen s.n.* and *Cowen 1509* (P!); and fig. 76, p. 100 in McDougall and Baggle, 1936]. Thus the flower description, both as to size, internal structure (gynophore!) and erose-fimbriate margin, the fact that there are no other species of *Gentianopsis* in the region, and the very specific habitat information leave no doubt whatsoever that *G. thermalis* is conspecific with *G. elegans*, and thus the valid name of what has generally been called *G. elegans*.

17. GENTIANOPSIS **macrantha** (D. Don) Iltis, comb. nov.

Gentianella macrantha D. Don, ex G. Don, Gen. Syst. 4:179. 1838.
Gentiana superba Greene, Pittonia 1:155. 1888.

The original description of *G. macrantha* leaves no doubt that its "corolla [has] . . . fringed segments" . . . Since there are only two Fringed Gentians in Mexico and *G. lanceolata* is not fringed, the name *G. macrantha*, clearly belonging to the northern taxon, because of priority should be utilized. Search in European herbaria should reveal a Sessé and Mocino type; yet a recent search of the Geneva, the British Museum, and Paris herbaria did not turn up such a collection.

18. GENTIANOPSIS **lanceolata** (Benth.) Iltis, comb. nov.

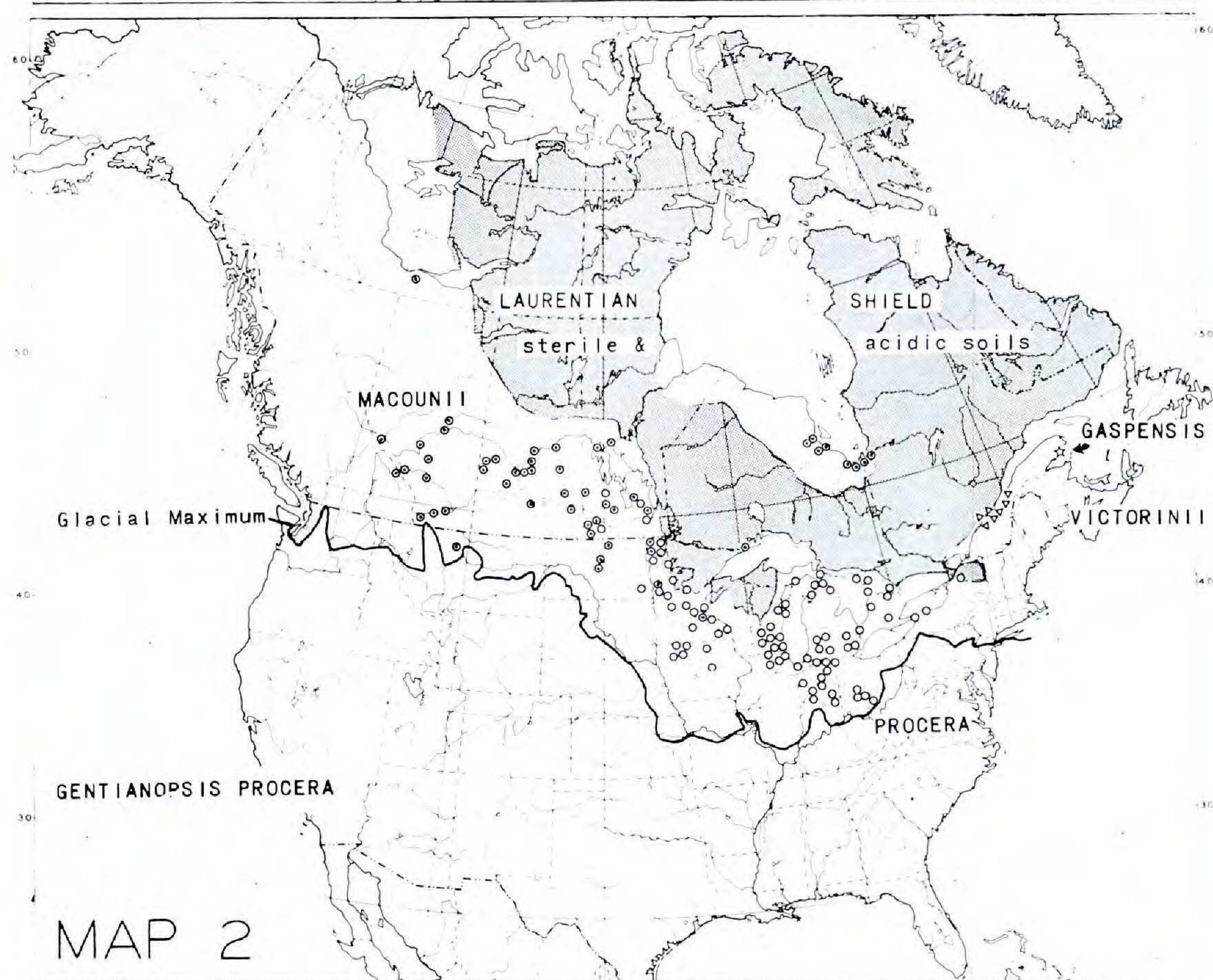
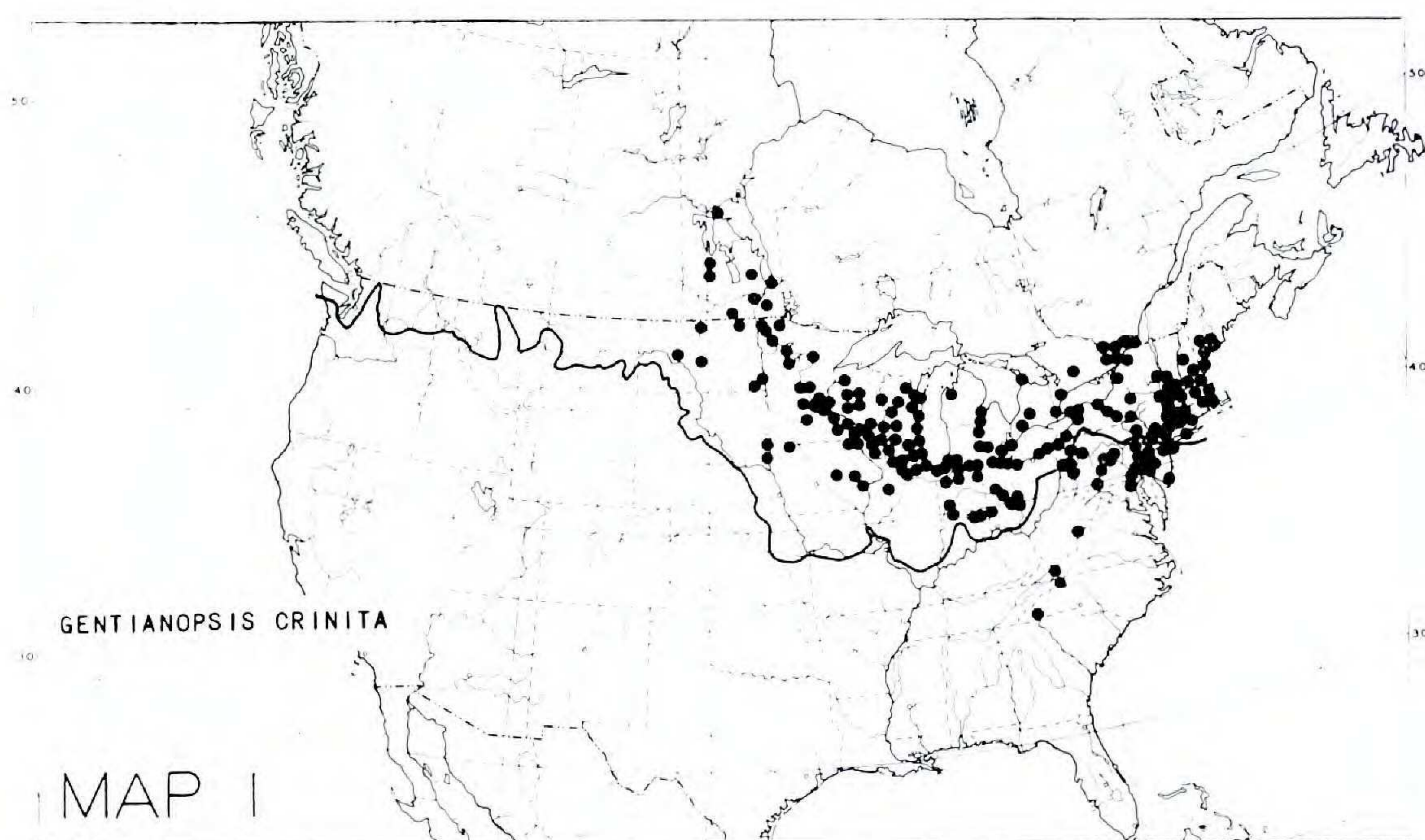
Leianthus lanceolatus Benth., Pl. Hartw. 24. 1839.

Gentiana macrocalix Lex. may well belong here. While the description is not clear and its type is lost, its "Habitat prope Vallisoletum et Irapaeum" would suggest affinity to the Southern Mexican *G. lanceolata* rather than the Northern Mexican *G. macrantha* (*G. superba*), since "Vallisoletum" refers to Morelia (Fide McVaugh) and "Irapeo" is a settlement west of Toluca (ca. 19°N, 100W), both south of the range of *G. macrantha*.

19. GENTIANOPSIS **holopetala** (A. Gray) Iltis, comb. nov.
Gentiana serrata Gunn. var. *holopetala* A. Gray, Bot. Calif. 1:481. 1876.
Gentiana holopetala (A. Gray) Th. Holm, in Ottawa Naturalist 15:110. 1901.
20. GENTIANOPSIS CRINITA (Froel.) Ma, loc. cit. 1:19. 1951.
Gentiana crinita Froel. Gent. Diss. 112. 1796.
21. GENTIANOPSIS CRINITA (Froel.) Ma, f. **albina** (Fern.) Iltis, comb. nov.
Gentiana crinita Froel. forma *albina* Fern. in Rhodora 19:152. 1917.
 Albino plants of *G. procera* are also known (though as yet not formally recognized), from Bailey's Harbor, Door County, Wisconsin, from color photographs (WIS!) taken by Karl Bartel of Blue Island, Illinois.
22. GENTIANOPSIS PROCERA (Th. Holm) Ma, loc. cit. 1:19. 1951.
Gentiana procera Th. Holm, in Ottawa Naturalist. 15:111. 1901.
 It is of interest, especially to one working with Wisconsin plants, that an Increase A. Lapham sheet originally in the C. W. Short herbarium, but now in the Paris herbarium, and collected ca. 1840 or 1850, says "Gentiana, a new species from Wisconsin."
23. GENTIANOPSIS **victorinii** (Fern.) Iltis, comb. nov.
Gentiana Victorinii Fern., Rhodora 25:87. 1923.
24. GENTIANOPSIS **macounii** (Th. Holm) Iltis, comb. nov.
Gentiana Macounii Th. Holm, Ottawa Naturalist 15:110. 1901.
Gentiana gaspensis Vict. Contr. Lab. Bot. Univ. Montreal 20:10. 1932.
25. GENTIANOPSIS **barbellata** (Engelm.) Iltis, comb. nov.
Gentiana barbellata Engelm., Transact. Acad. Sci. St. Louis 2:216. 1862.
26. GENTIANOPSIS **simplex** (A. Gray) Iltis, comb. nov.
Gentiana simplex A. Gray, Newberry, Bot. Rept. U.S. Pac. R.R. Survey 63:87. 1857.

II. THE FRINGED GENTIANS EAST OF THE ROCKY MOUNTAINS

The Eastern and Middle-western Fringed Gentians, *G. crinita*, *G. procera*, *G. victorinii* and *G. macounii* (incl. the indistinguishable *G. tonsa* and *G. gaspensis*) have recently been treated in many different ways. Thus Fernald (1950) recognizes all of these as valid species of *Gentiana*, while Gleason (1952), in listing *G. crinita*, *G. procera*, *G. Victorinii* and *G. tonsa* (incl. *G. gaspensis*), comments (3:62) that "... [*procera*] and the next two species [*victorinii*, *tonsa*] are so closely similar that they might well be reduced to varieties of a single widely varying species." Gillett (1957, 1963) visualized an all-inclusive *Gentianella crinita*, composed of 4 equivalent subspecies, with *G. gaspensis*



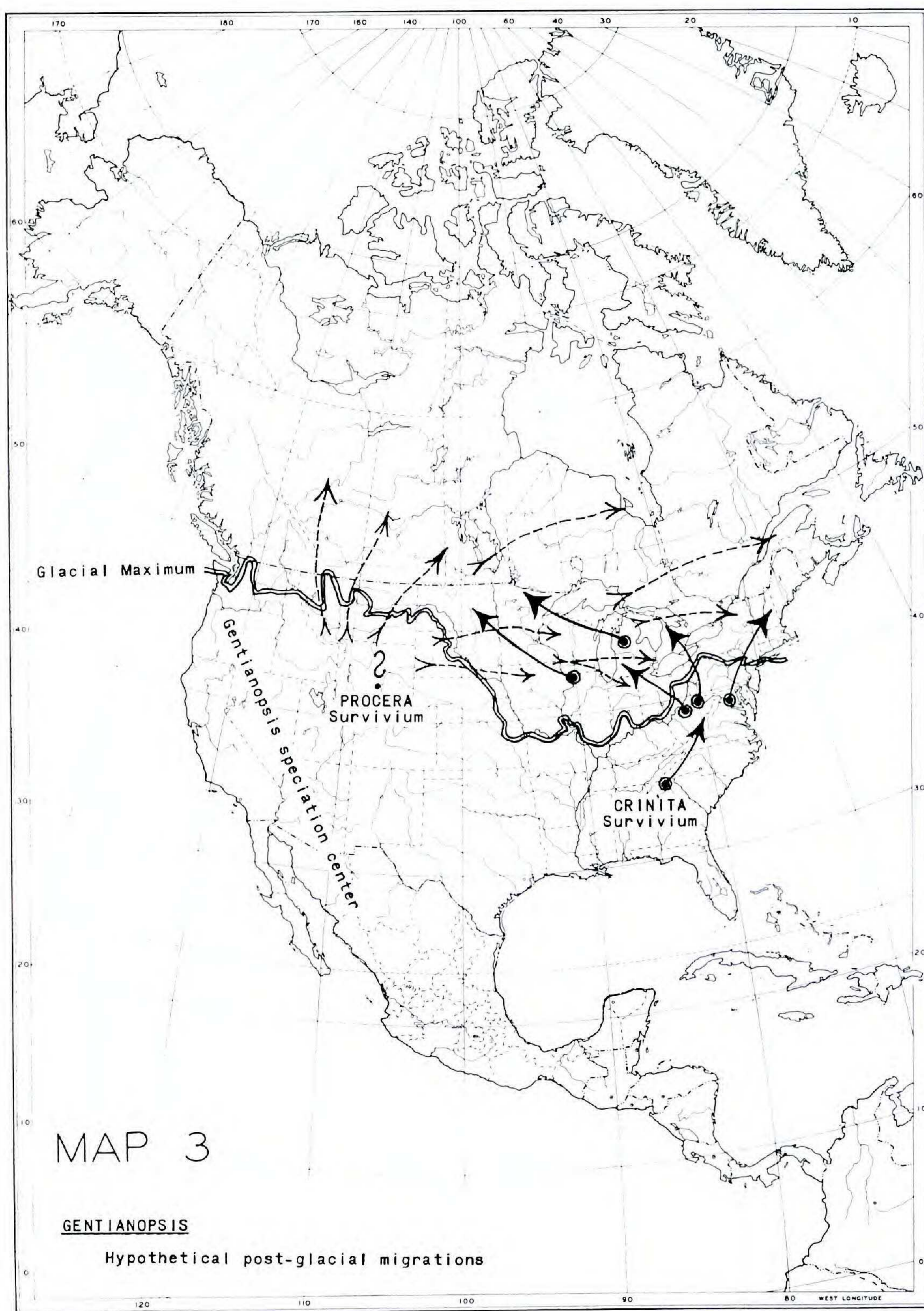
and *G. tonsa* synonymized under ssp. *macounii*. (Actually, many of Gillett's comments in the 1957 study make it obvious that he is in essential agreement with Gleason and the views presented here.) In evaluating the morphological features of these plants it became evident that neither

Fernald's "splitting" nor Gillett's "lumping" properly reflects the natural relationships of these taxa. Furthermore, a reconsideration of ecology, geography and morphology suggests a synthesis of the above viewpoints into a more natural and dynamic taxonomy (closely resembling the arrangement of Gleason), a system more compatible with evolutionary and historical factors. It will be maintained here that only two species should be recognized, the distinctive and rather stable *G. crinita*, and the variable *G. procera*. The latter includes all the other taxa mentioned above, some clinal, others discrete local populations, which might, if needed, be recognized at most as weak varieties.

The following remarks are partly based on field observations of Wisconsin and Michigan plants (cf. Mason and Iltis, 1965), and are partly the result of editing two studies on Wisconsin *Gentianaceae* (by J. S. Pringle, 1964, 1965).

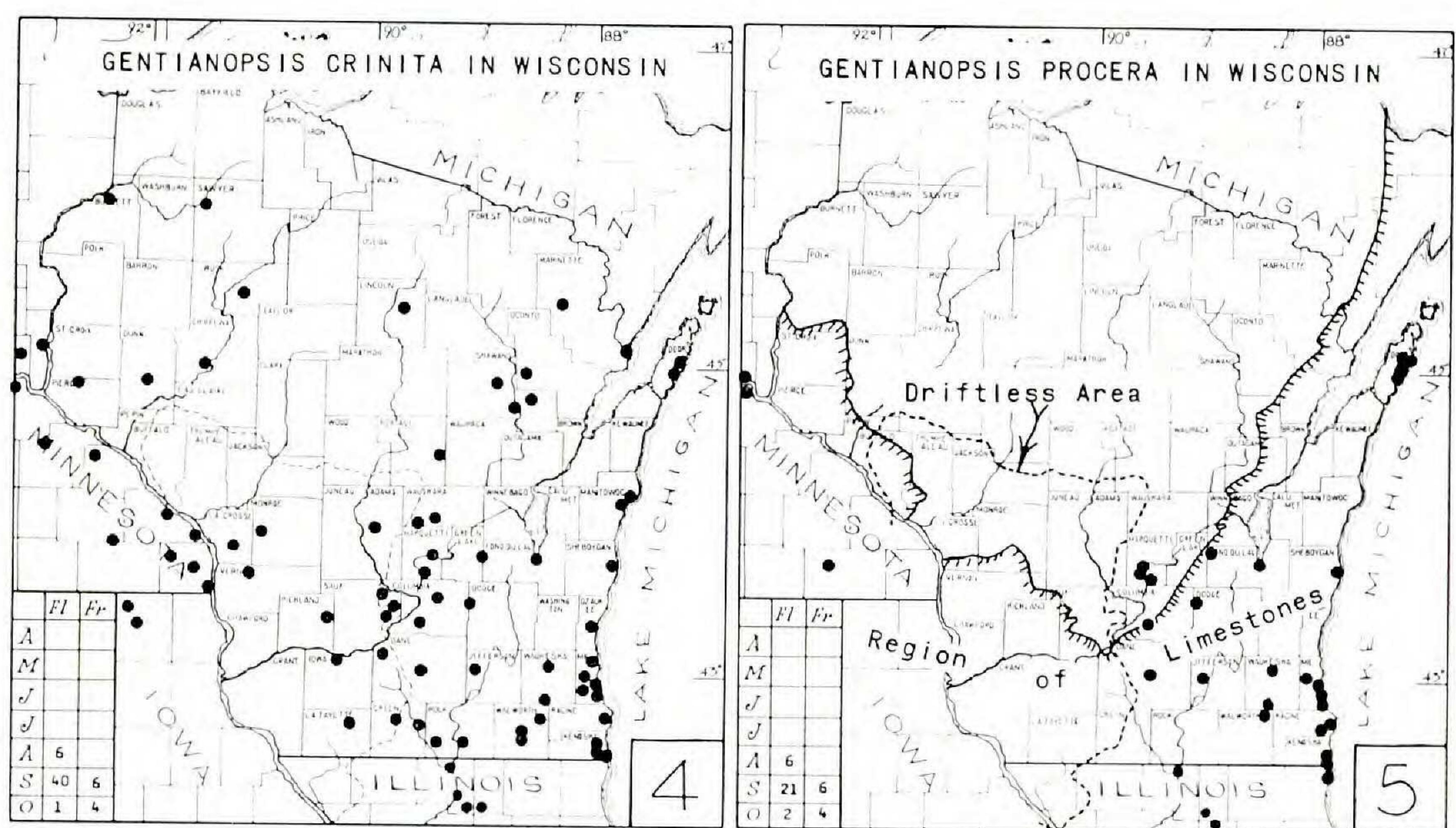
In Wisconsin and the Middle West in general, *G. crinita*, *sensu stricto*, is widely distributed (Map 4) and locally common to rare in marshy or sandy sedge meadows, swales and moist dunes, damp open woods, seepage slopes, dolomitic sandstone cliffs, and low wet sandy flats on Lake Michigan shores, there with *Parnassia caroliniana*, and on low calcareous prairies, apparently not requiring, but tolerating, as calcareous a habitat as *G. procera*.

The closely related, sometimes very similar *G. procera* (Map 5), on the other hand, is much more locally distributed in Wisconsin than *G. crinita*, though, as on the Kenosha Prairie, Lake Wingra Marsh (Dane Co.) and Ennis (Muir) Lake Fen (Marquette Co.), the two species may sometimes grow together or near each other. *Gentianopsis procera*, in contrast to *G. crinita*, prefers *distinctly* alkaline habitats (as judged from associated plants), such as calcareous or marly, often springy, low prairies or sedge meadows, which in Wisconsin and Iowa have sometimes been referred to as "fens" (Anderson 1943, Curtis 1959), or moist calcareous (Niagara Dolomitic) sands on Lake Michigan shores, as at Bailey's Harbor, Door Co., (there with *Gentianella quinquefolia*, soil pH 8, *fide* Fuller), and springy seepage on the Lake Michigan bluffs (pH 7, *fide* Pohl). These usually wet calcareous sedge prairies or fens, which are best developed on calcareous drift derived from the Niagara Dolomite, on the dolomite itself, or around calcareous springs, are characterized by a distinctive assemblage of calciphiles whose distribution patterns often closely resemble that of *G. procera*. These include *Solidago ohioensis*, *S. riddellii*, and perhaps *S. patula* (Salamun 1963), *Salix candida* (Argus 1964), *Lysimachia quadriflora* (Iltis & Shaughnessy 1960:133), *Lobelia kalmii*, *Aster junciformis*, *Parnassia caroliniana*, *Potentilla fruticosa* (Mason & Iltis 1958: Map 16) *Valeriana ciliata* (*V. edulis*), the rare *Scleria verticillata* (cf. Iltis 1957) and others. All of these together with *G. procera* are rare or absent from the Driftless Area



of SW Wisconsin, not apparently because of any historical factors or absence of calcareous rocks, but because of deficiency in moisture, of flat marly springs and seepage, and wet calcareous glacial till.

Gentianopsis procera flowers in Wisconsin from (mid-) late August



into early October, with a peak in the *second week* of September, apparently blooming just a little earlier than *G. crinita* (which blooms from mid-August into October, with a peak in the *second and third week* of September), a fact mentioned for Indiana by Deam (1940) and for the Northeastern United States by Fernald (1950).

In Minnesota, where the overall occurrence of the two species is similarly scattered, the detailed ranges (courtesy Dr. J. Moore) show that only in a few instances do the species grow near each other, with a tendency for *G. crinita* to grow in the eastern, more wooded, moister areas, *G. procera* in the western, more open, drier prairie sections of Minnesota. Similar comments apply to Iowa (cf. Anderson 1943; Beal and Monson 1954:76, map 182).

In Indiana, Deam (1940) reports that, when the two species occur together, *G. procera* prefers moister sites. The same can be said for Wisconsin.

The striking absence of *G. procera* from interior Ontario and Quebec south of Hudson Bay (cf. Map 2) is no doubt due to the absence of calcareous rocks, a fact of great phytogeographical importance first pointed out by Wynne-Edwards (1937:24, map 2). As a matter of fact, the contrasting ecological behavior is well brought out by a comparison of not only the Wisconsin map (Map 5), where all *G. procera* stations are either over dolomite or near calcareous springs, but also by their total distribution (Map 2). For here we can see that *G. procera* follows the Niagara dolomite from Wisconsin across Upper Michigan to the Bruce Peninsula of Ontario and beyond to Niagara Falls, a region through most of which *G. crinita* is lacking (Map 1). Though the species at rare times do occur together in the Middle West and show some over-

lap in blooming periods (as seen in herbarium records), there is only indirect and inconclusive evidence that hybridization or introgression has taken place between them (see below), their distinct geographic patterns, ecology, genetic behavior, seasonal isolation and morphology suggesting two clearly marked, well isolated taxa.

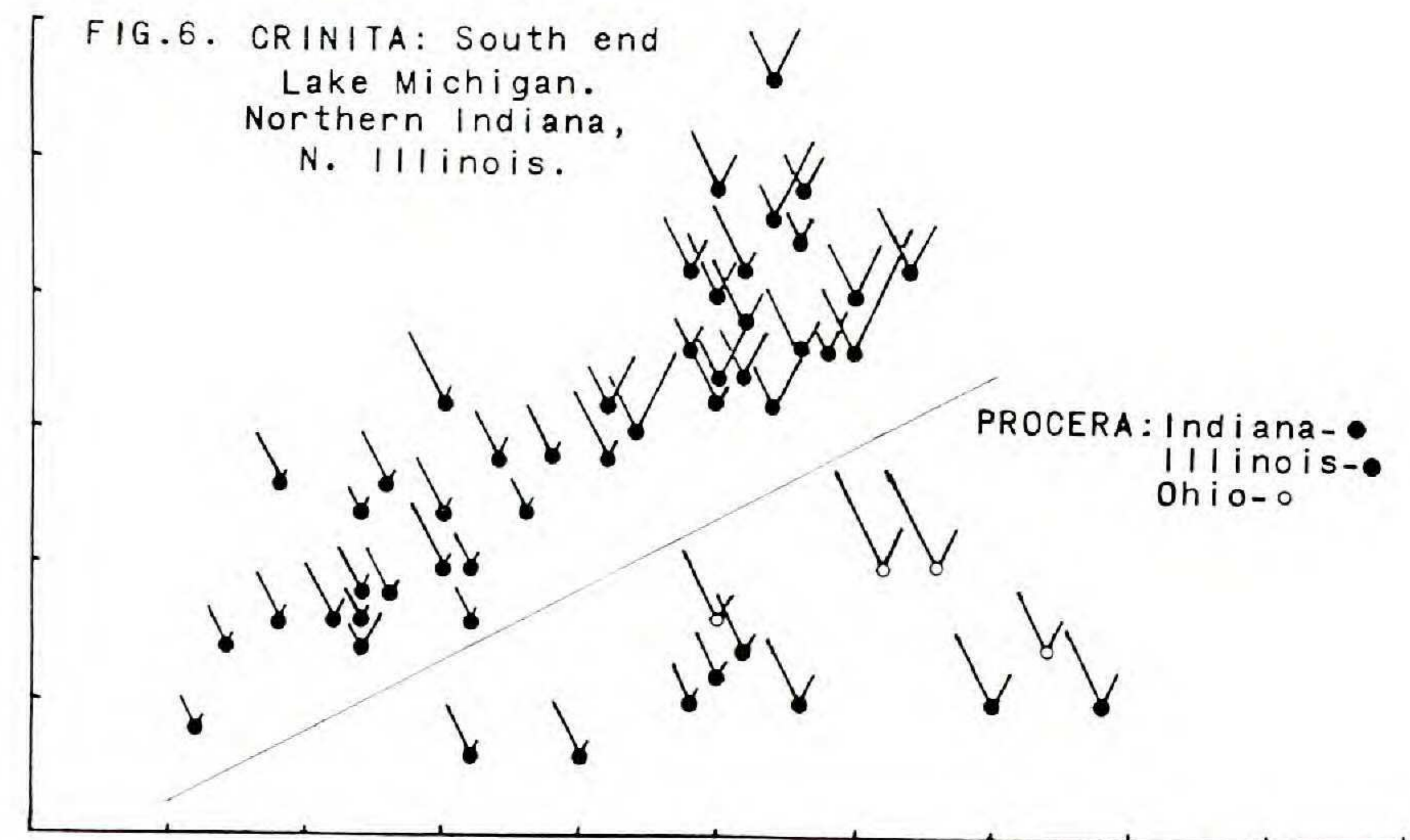
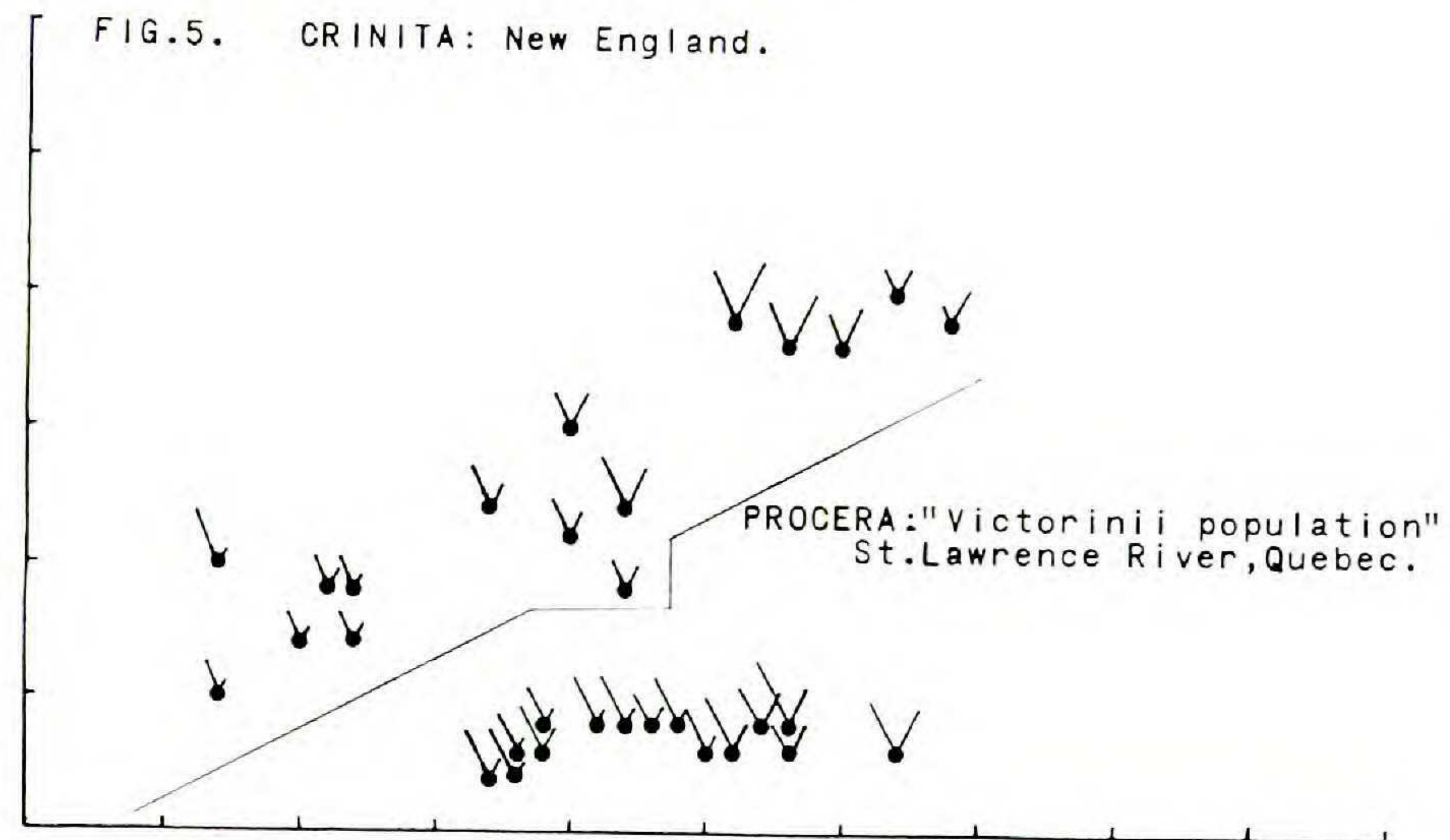
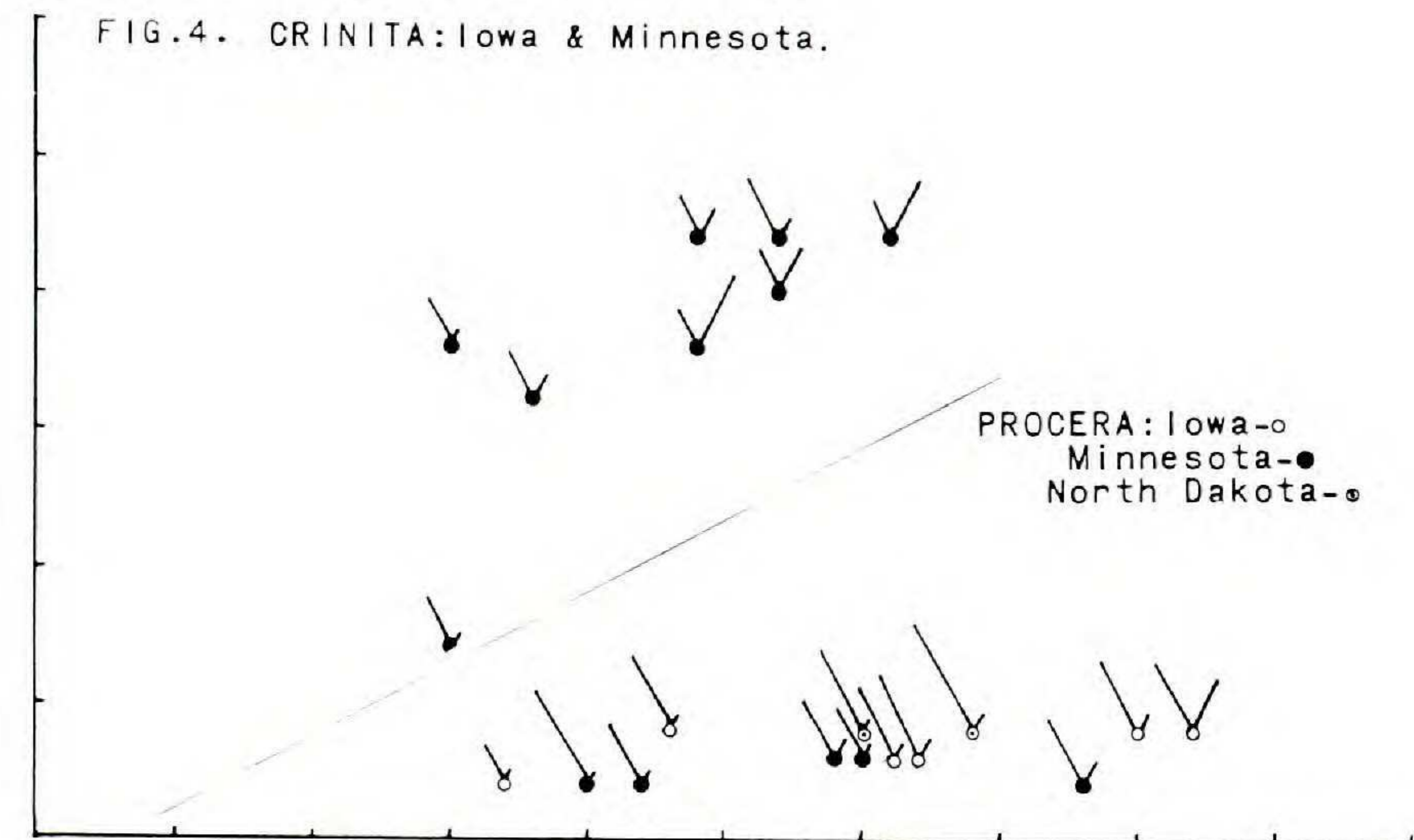
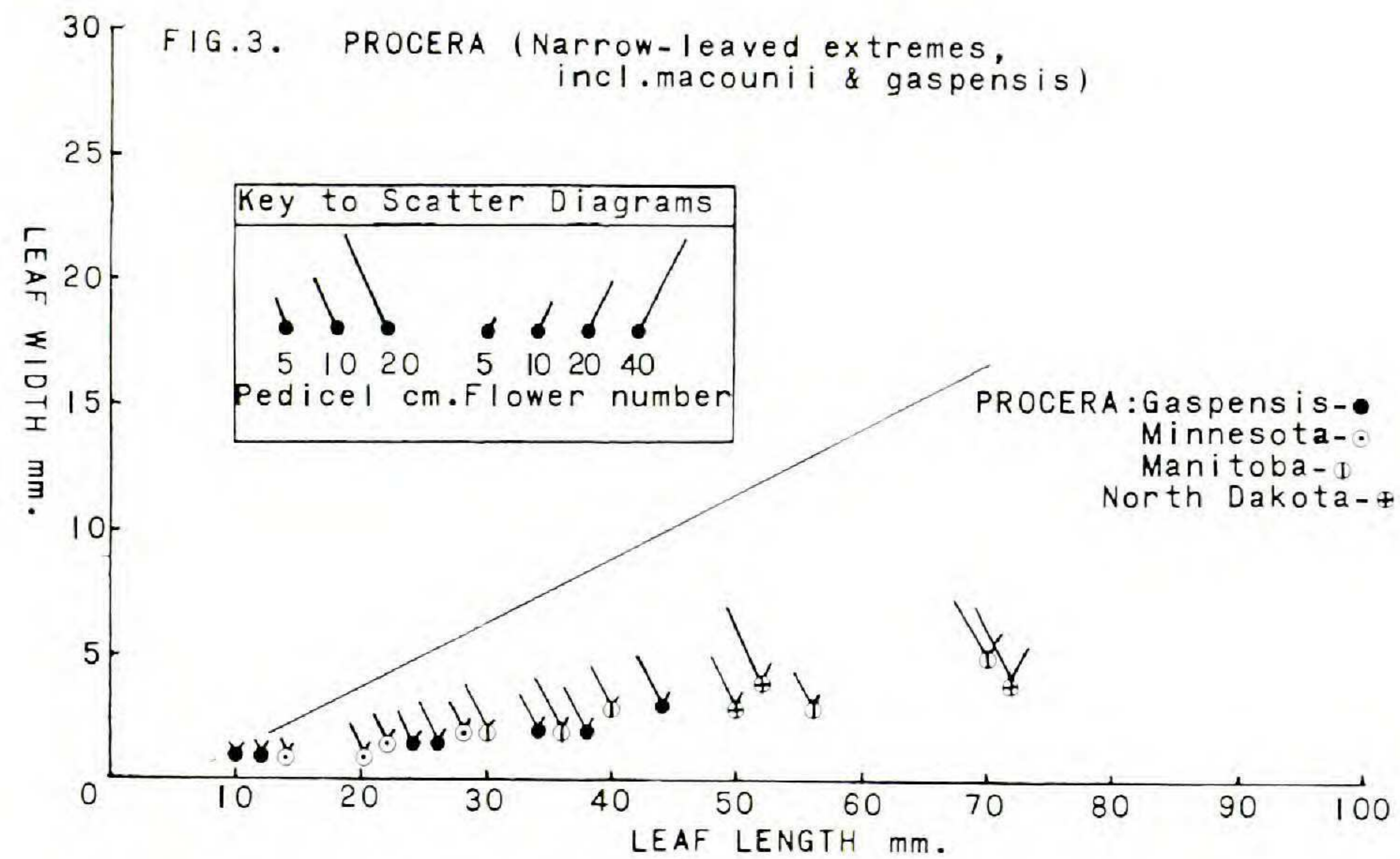
What relationship do *G. crinita* and *G. procera sensu stricto* have to the other Eastern taxa of *Gentianopsis*? Herbarium specimens, or the exquisite illustrations in Gillett's 1963 study, clearly show *G. crinita* to be relatively unique, while *G. macounii* (incl. *G. gaspensis*), *G. procera* and *G. victorinii* form a unified series of morphologically either essentially identical or completely confluent populations, with only minor quantitative differences between them. To understand the variation patterns it is well, however, first to represent the local or regional populations on scatter diagrams, second, to explain some of the anomalies shown in these scatter diagrams in terms of taxonomy, climatic trends and possibly introgressive hybridization, and last, to synthesize all data in historical perspective.

CHARACTERS USED IN SCATTER DIAGRAMS

The following scatter diagrams show graphically and quantitatively the differences between *G. crinita* and the other taxa, and demonstrate the morphological congruence of the members within the *G. procera* complex. Of the many morphological features cited in the literature, only few were found to be of value. Thus flower size, plant size, length of petal cilia, and extent of and scabrosity of calyx keels are characters sometimes used, but difficult to evaluate on herbarium material and are of limited biological significance.

The following characters were used in the scatter diagrams: 1) the relationship of leaf length to width of the median leaves (*longest leaf subtending the first flowering branch of each plant*), which seemed to vary least with plant size (the lowermost leaves cannot be used as they are nearly identical in all taxa); 2) The measure of the longest pedicel of each plant, which is related sometimes (in small plants) to plant size but which differs significantly between the *G. procera* complex (long) and *G. crinita* (generally short); 3) flower number generally low in *G. procera*, and high in *G. crinita* (1 to 176!, according to Fernald 1950).

Each glyph represents one plant, with each millimeter on the left glyph arm equalling 3 cm of pedicel length, while each mm on the right arm equalling 6 flowers. The slanted line bisecting the scatter diagram indicates the division between *G. crinita* and *G. procera*. Thus, taking the attributes of the two taxa in consideration, the glyphs of *G. procera*, even when very close to this dividing line, will generally have very long pedicels (long left glyph arm) and very few flowers (short right glyph arm), while in *G. crinita* glyphs it will be the reverse. There are of course very robust *procera* giants with many flowers, and



occasional small *crinita* plants with only one flower, these then often with rather long pedicels. Distinctions between species break down in the smallest depauperate plants (cf. Figs. 3, 8, and 9, lower left corner), whose identification is often only possible in conjunction with normal plants of the same population (see Fig. 9).

Though only material from the University of Wisconsin Herbarium was used (truly a major limitation), the resultant graphs nevertheless clearly illustrate many of the relationships of these taxa. Grateful acknowledgement is due to Dr. Gillett, who in 1956 and 1957 named nearly all our material, and whose names have been followed in nearly all cases.

DISCUSSION OF THE SCATTER DIAGRAMS. (Figs. 3-10)

Fig. 3. *G. macounii* (incl. the very local, quite indistinguishable *G. gaspensis*). Solid dots are *G. gaspensis* (Victorin et al. 4008), the hollow dots collections one each from Minnesota, North Dakota, and Manitoba. The Gaspé plants (triangles on Map 2) are generally smaller, and have narrower and shorter leaves. However, the variation pattern is continuous with that of plants from Minnesota and further west. All plants have very few flowers, and, except for the very slender depauperate ones, usually have long pedicels. These are the narrow-leaved extremes of the *G. procera* complex.

Fig. 4a. *G. procera* in Minnesota, Iowa and North Dakota. Except for being a little more robust and wider-leaved (hence their identification as *G. procera*), sometimes with longer pedicels and/or more flowers (e.g. the far right glyph), none of these plants differ in any marked way, either in the herbarium or on the graph, from the plants named *G. macounii* of Fig. 3.

Fig. 4b. *G. crinita* in Minnesota and Iowa is sharply distinct from *G. procera*, and graphs essentially as other *G. crinita* collections, such as those from New England (Fig. 5).

Fig. 5a. *G. procera* (*G. victorinii* population from the shores of the St. Lawrence River, Quebec; cf. Fig. 2). These differ in no marked way from the *G. procera* of Fig. 4, except that the glyphs are grouped more closely together, indicating lower variability.

Gentianopsis victorinii grows on the twice-daily inundated, nearly bare limestone slabs of the fresh-water intercotidal zone along the St. Lawrence River. *Gentianopsis gaspensis* (unless one wishes to follow some Canadian authors who consider the Hudson Bay populations *G. gaspensis* also) is restricted to a minute area of brackish "marshland" or open gravelly grassy "swale" at the mouth of the Bonaventure River near the tip of Gaspé Peninsula. Both populations are limited to local and ecologically open environments. Though a great deal has been made of the peculiar habitat of *G. victorinii* (Rousseau 1932—who reports a pH of 7.5; Raymond 1951; Marie-Victorin 1938), this is not too different

FIG. 7. PROCERA: Michigan & adjoining Ontario.

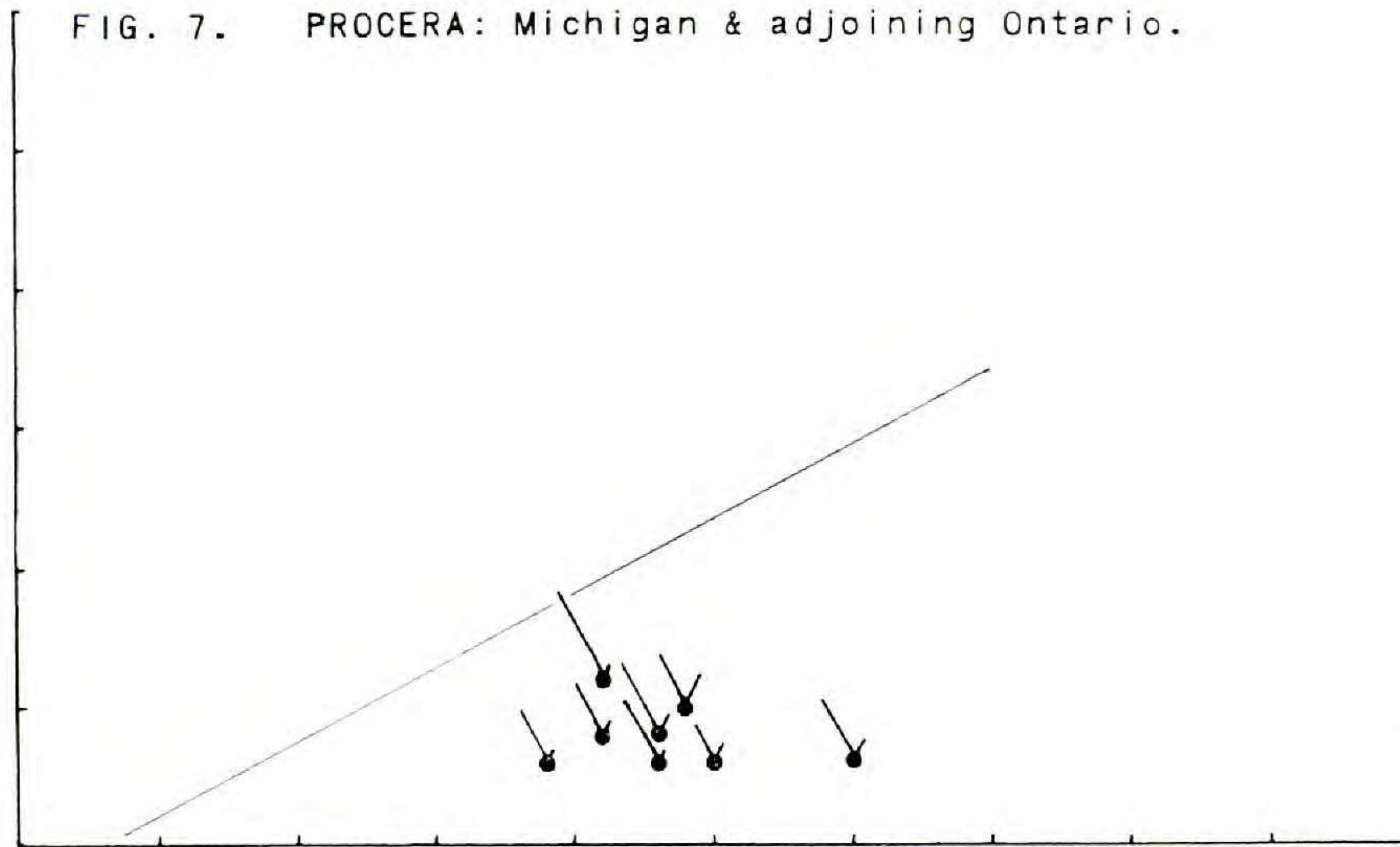


FIG. 8. CRINITA & PROCERA in Wisconsin.

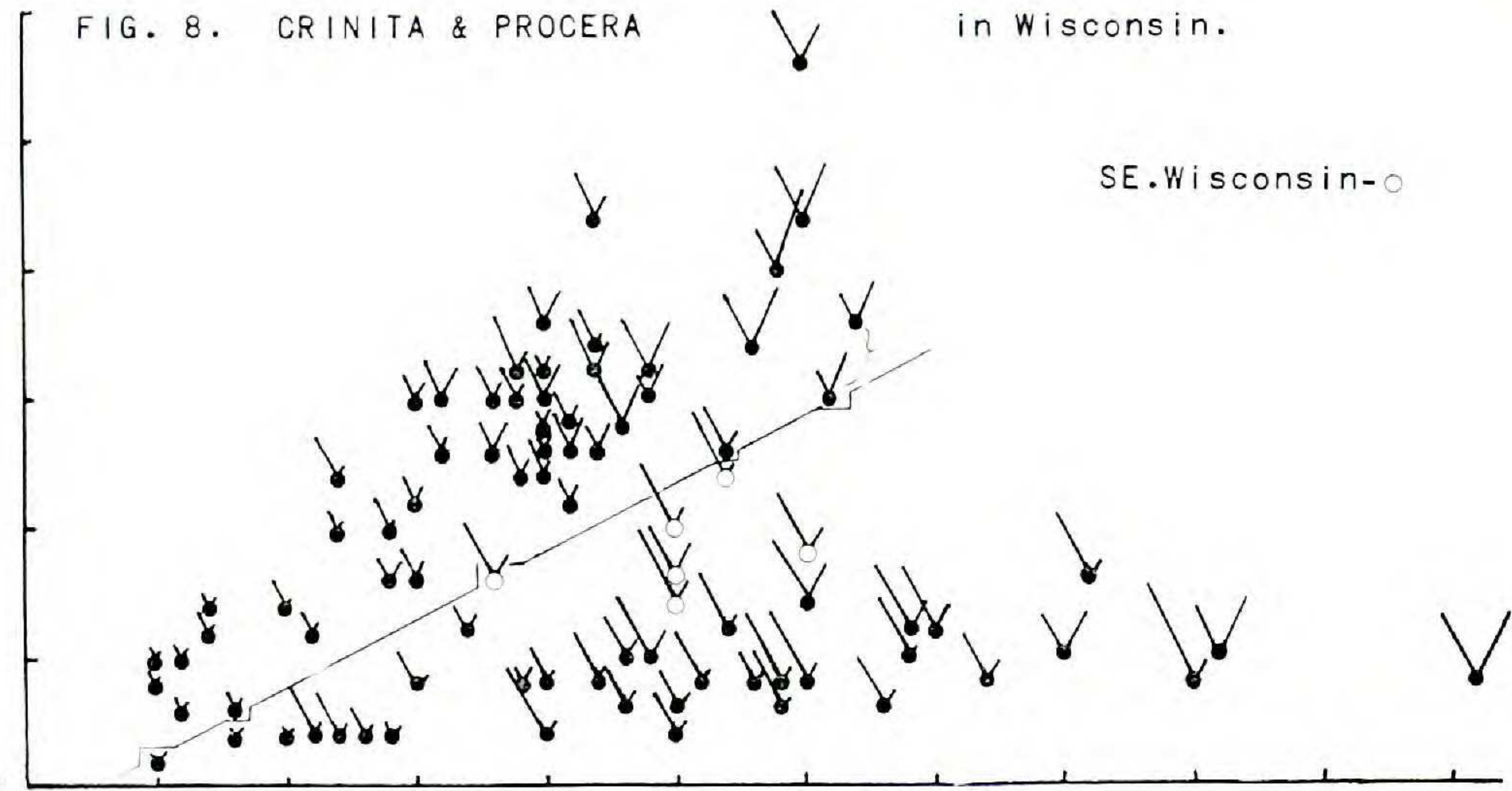


FIG. 9. MASS COLLECTIONS FROM WISCONSIN.

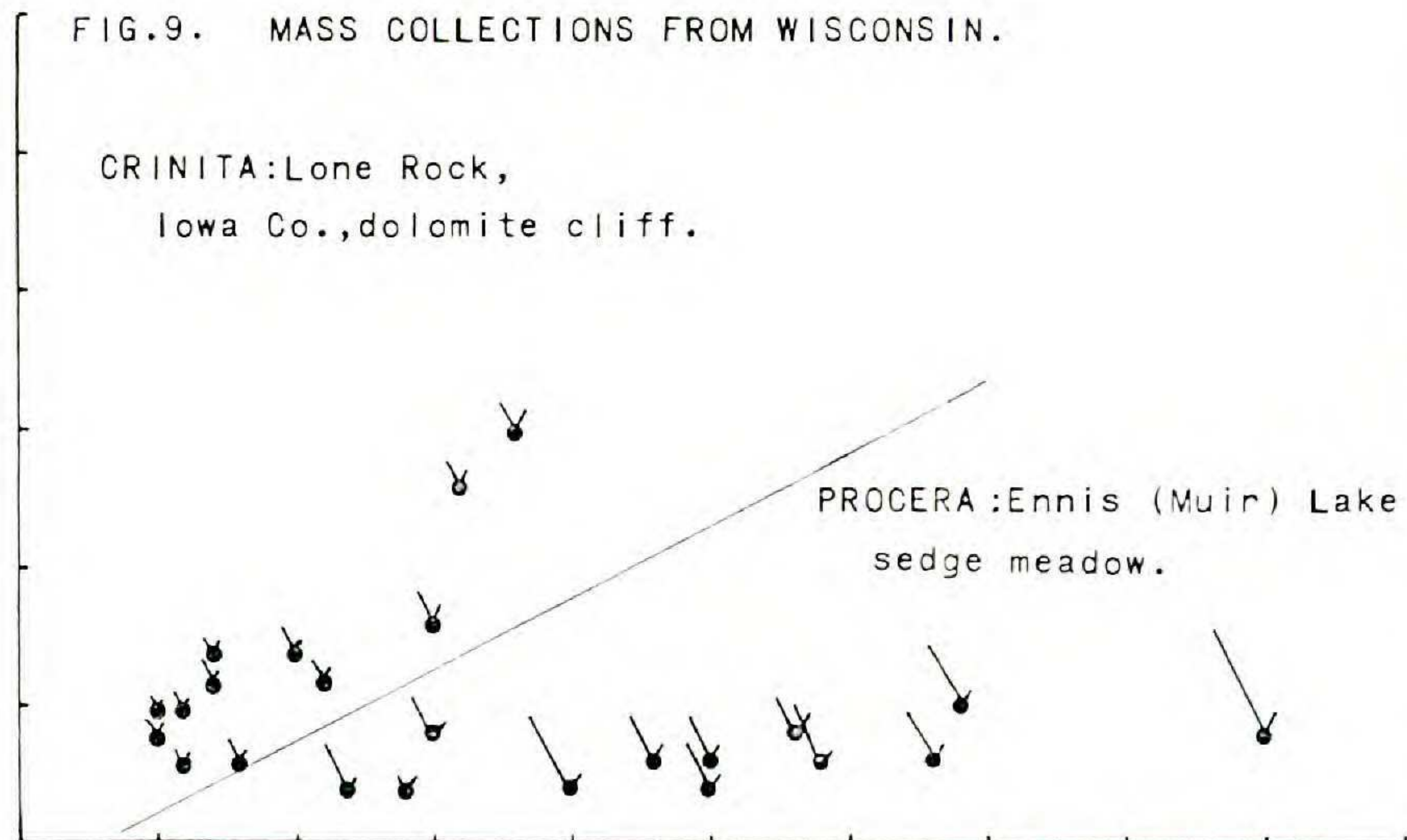
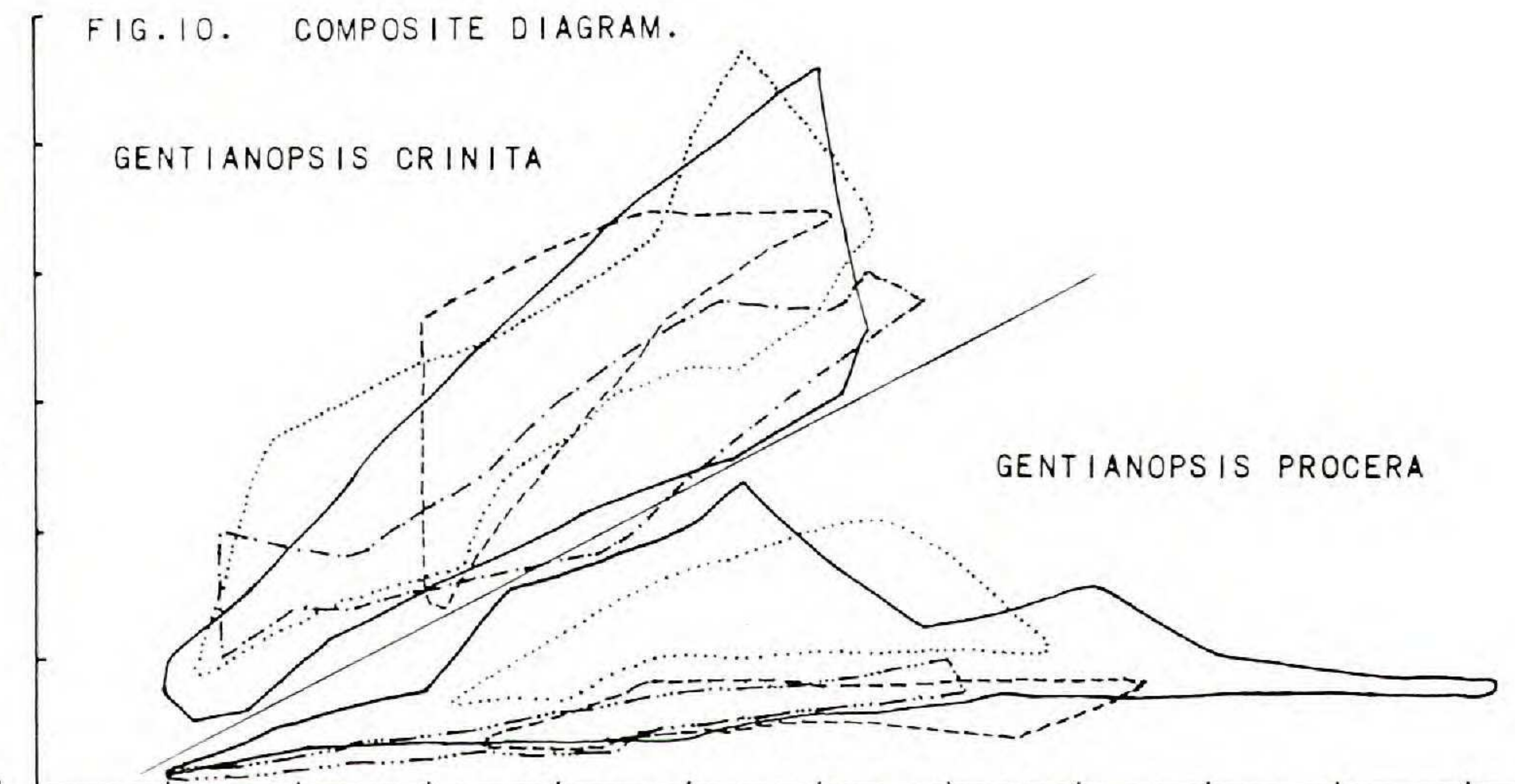


FIG. 10. COMPOSITE DIAGRAM.



from the moist, spring-submerged calcareous sedge meadows of the Kenosha Prairie in Southeastern Wisconsin, which, very shallowly underlain by Niagara Dolomite in places covered with Fringed Gentians in the fall, represents one of the most interesting Middle-western habitats and now is threatened with total extinction.

The apparent uniformity of both the *G. victorinii* and *G. gaspensis* populations, which must have played its part in their being described to begin with, as well as their specialized habitat and great local restriction can be explained by either considering them 1) "Founder populations" (Mayr 1963; Goodhart 1963), founded, as it were, by one or few accidentally dispersed seeds which then expanded into rather small, relatively homogenic populations, remarkably uniform in ecological tolerance and morphology and therefore distinctive in aspect (hence the temptation to call them species) or, less likely, 2) by considering, in addition, their specialized and rather uniform calcareous habitats which would result in selection of uniform types. The small size of these populations, which would permit random genetic drift to operate, may also be significant. It is doubtful, however, whether these micro-neoendemics should be accorded any taxonomic status beyond the informal "*victorinii* population" or "*gaspensis* population." In this connection, Gillett's comment (1957:228) that "subspecies *victorinii* is morphologically somewhat intermediate between ssp. *procera* and ssp. *macounii* . . ." is to the point, and suggests that all these should simply be considered as but one species.

Fig. 5b. *G. crinita* from New England. Some of the Massachusetts *G. crinita* collections, which presumably are free of introgression from *G. procera* (which doesn't grow here), are similar in leaf shape to wide-leaved forms of *G. procera*, indicating perhaps that though overall modes of growth of the two taxa differ, occasional genotypes under certain environmental conditions may copy and approach the phenotype of the other species.

Fig. 6a. *G. procera* from Indiana, Illinois (black glyphs) and Ohio (hollow circle glyphs). Note the often larger leaf-width of the *G. procera* collections as compared with those from further west (Figs. 3 and 4). The Ohio specimens, especially, are very robust (collections of C. W. Short, "Columbus" 1835, "Prairies of Ohio" 1836). The glyph position on the diagram should be related to the robustness of these plants (flowers to 8 cm long! pedicel to 19 cm long!).

Fig. 6b. *G. crinita* from the south end of Lake Michigan (mostly Northern Indiana collections of L. M. Umbach). The distribution of glyphs is nearly identical to those from Wisconsin or New England.

Fig. 7. *G. procera* from Michigan and adjoining Ontario. A very small sample of 3 collections.

Fig. 8b. *G. crinita* in Wisconsin follows exactly the same distribution

as in other parts of Eastern North America (see Fig. 10). In short, there appears to be no great influence of either climate or of genetic introgression from *G. procera* on phenotypic expression in *G. crinita*. The fact that the glyphs go to the far left-hand corner is explainable by the particular depauperate cliff population ("Lone Rock"), plotted separately in Fig. 9.

Fig. 8a. *G. procera* in Wisconsin is more complex. First of all, there are many plants that are as narrow-leaved and few-flowered as some of the *G. macounii*-*G. victorinii* specimens plotted in Figs. 3, 4, and 5. Most plants, however, have much wider leaves than those of *G. Macounii* or *G. procera* in Figs. 3 and 4, and are similar to those shown in Figs. 6 and 7. The question arises, whether this increase in leaf-width is related to the moister Wisconsin climate, or to introgression from *G. crinita*. Nearly identical broad-leaved types, again all very robust plants, are shown in Fig. 6 from Ohio. Were we to remove from Fig. 8 the generally robust plants from Racine, Kenosha and Milwaukee County (marked by hollow circles) the separation of the two taxa would be much clearer. Again, these few plants grow close to the Lake Michigan shore in Southeastern Wisconsin in a relatively mild climatic regime. At the same time, it is also a region where *G. crinita* overlaps the range of *G. procera*! Perhaps the broad-leaved phenotypes in this region represent in part phenotypic responses of the narrow-leaved genotype to climatic factors and in part introgression from *G. crinita*.

Fig. 9. *G. crinita* and *G. procera* in Wisconsin: Mass collections to show variability within single populations. Fig. 9a. The *G. crinita* collection from Iowa Co., across the Wisconsin River from Lone Rock, Wisc., is peculiar in that these mostly depauperate plants grow on a vertical North-facing dolomitic sandstone cliff. Collections made there in 1925 by N. C. Fassett and again in 1958 by Brian McNab show precisely the same morphological distribution.

Fig. 9b. *G. procera* population from an alkaline sedge meadow ("fen") on Muir (Ennis) Lake, Marquette County: note large spread of glyphs within this local population.

Fig. 10. Composite of all graphs of *G. crinita* and *G. procera*. See discussion especially of Figure 6. *G. victorinii* not shown since its limits are essentially congruent with those of the western plants of *G. procera* (dashes).

In summarizing these 8 graphs it can be said that 1) *G. procera*, *G. macounii*, *G. victorinii* and *G. gaspensis* must be considered as synonymous, the latter two evidently representing nearly homogenic small populations, originally established by long-range dispersed single or few seeds, hence low in variability as well as probably strongly selected by local conditions; 2) of these taxa, *G. procera* is the widest-leaved, intergrading gradually and completely into the more narrow-leaved western

macounii. In Wisconsin and Indiana, only very robust plants resemble plants of *G. crinita*. Since there is a West to East clinal increase in leaf-width and robustness in the *macounii-procera* complex, but not a corresponding decrease in leaf width from East to West in *G. crinita*, it would seem that *G. procera-macounii* has shown itself sensitive to increase in moisture relations eastward by an increase in leaf width, this trait possibly becoming stabilized by selection in Southeastern Wisconsin or Northern Indiana. The alternative hypothesis, namely introgression with *G. crinita* as a cause for increase in leaf width, may also play a part, yet *G. crinita* does not approach *G. procera*; 3) Though local populations tend to be variable, the scatter diagrams show clearly the presence of two modes of variation in this complex, with few if any intermediates. It would seem best, therefore, to recognize as species only *G. crinita* and *G. procera*, the latter with some variable and isolated populations perhaps deserving names for purposes of discussion, but whose close biological interrelationships need be clearly recognized.

III. PROBABLE HISTORY OF GENTIANOPSIS IN THE EASTERN UNITED STATES

Since the modern distributions of *G. crinita* and *G. procera* (*sensu lato*) must be related to Pleistocene glaciation, we can visualize their post-glacial emigrations from glacial survival centers (Hulten 1937) or "survivia," and attempt to reconstruct their post-glacial history (Map 3). All factors of distribution, ecology, phenology and even morphology, suggest that these two taxa are the result of separation by the Pleistocene glaciers of a once widespread ancestral species into two populations—one surviving in the longer growing season of the moister, more acidic Appalachian region in the East, and evolving into a broad-leaved, many flowered, late-blooming *G. crinita*; and one in the shorter growing season of the drier, more alkaline upper Great Plains (and Northern Rocky Mountains?) in the West, and evolving into a narrow-leaved early- and few-flowered heliophilic, calcophilic *G. procera*. Post-glacially, the eastern *G. crinita* spread into the glaciated region of the "White Pine-Hemlock-Northern Hardwoods" and beyond, while the western taxon (or were there several, morphologically slightly differentiated, geographically isolated surviving populations?), which, in its more depauperate, xeromorphic, Northern Great Plains phase is known as *G. macounii*, migrated eastward, especially on damp, but physiologically dry (?), alkaline (calcareous) habitats, to overlap the range of *G. crinita*. In Wisconsin and Michigan the higher precipitation (?) resulted through selection or phenotypic response in generally larger, bigger-leaved plants which have been formally distinguished from *G. macounii* as *G. procera*. Some of these resemble *G. crinita*, suggesting the possibility of introgression from *G. crinita*. While the scatter diagrams reflect this simi-

larity, it seems more reasonable to suppose that increased leaf size may be a phenotypic response to moister habitat, less alkaline soil and/or longer growing season.

The Wisconsin and Indiana *G. procera* populations are rather variable, suggesting broad dispersal, "en masse" migration and many genotypes. The Eastern Canadian populations in contrast, are very uniform. As is characteristic of many other Western elements, *G. procera*-*G. macounii* spread as far east as the Gaspé Peninsula and Hudson Bay, probably by sporadic long range dispersal. The resultant isolated and highly local, ecologically specialized, genetically evidently impoverished and homogenic populations have been taxonomically recognized as *G. gaspensis* and *G. victorinii*, two neo-endemics perhaps best considered as weak varieties or just populations of *G. procera* (cf. Mason and Iltis, 1965).

There are, of course, examples of quite distinctive species or subspecies evolving in as short a time as 10,000 years or less in the Northeastern United States. One need only examine some of the Great Lakes endemics, e.g. *Iris lacustris*, *Hypericum kalmianum*, *Cirsium pitcheri* (cf. Johnson and Iltis 1963:290-292), *Calamovilfa longifolia* var. *magna* (Thieret 1960), or *Agropyron psammophilum* (Senn and Gillett 1961). However, in comparison especially to the beach and dune species, the Fringed Gentian populations in question are not nearly as markedly differentiated. Thus, in the formation of these Post-glacial neo-endemics, evolutionary rates appear to have differed greatly, depending on the nature of the plants themselves, the type of habitat, the kind of selection and the original variability and size of the population.

It is of interest, that when Raymond (1951) described the habitats of these gentians, he listed *G. procera* together with other taxa he considers Cordilleran [i.e. western] elements, which in a sense *G. procera* is. To Marie-Victorin (1938:528) *G. victorinii* and *G. gaspensis* are a "... fascinating groups of plants, ... simultaneous endemics and relics, their Cordilleran affinity being evident in all cases." Gillett likewise emphasizes the complete intergradation of *G. macounii* into *G. procera*; and well he might! However, his other conclusion, that this cline continues to the Appalachians to include *G. crinita* has not been substantiated by the present study. That hybridization may occasionally occur seems, in view of their obvious relationship, probable. An interspecific "cline," however, represents a very different situation.

Subsequent to post-glacial dispersal and migration some 8000 or less years ago the forces of selection may have produced the cline from small-leaved forms in the drier West (*macounii*) to broad-leaved more robust forms (*procera*) in the moister Middle West and East. The processes of sporadic long range dispersal, however, may still continue to this day, and would explain narrow-leaved *macounii* extremes among otherwise typical *procera* as far east as Minneapolis (Rosendahl 4756, SW of Nichols,

Dakota Co. Minn. WIS!). The presence of narrow-leaved "*macounii*" plants in Gaspé, on the other hand, may simply be a reflection of the Atlantic Ocean's proximity and consequent halophytic conditions of the habitat, a habitat resembling saline marshes such as are found in Manitoba or Montana.

The fact needs be considered also that these are small-seeded, easily dispersed, "open habitat" annuals (or biennials), probably self-compatible, with rapidly fluctuating populations, a fact that would have bearing on evolutionary rates. Their population size during and immediately following the glacial retreat may have been locally enormous. Since then, through competition with forest or perennial communities, their numbers may have dwindled into the modern, localized populations in the East, many of which apparently became extinct in the last 100 years (e.g. New York stations of *G. procera* on Lake Ontario near Rochester; the sole West Virginia station of *G. crinita*, cf. Strausbaugh and Core 1958:732).

The ideas presented here no doubt represent great simplification. Thus there remains no clarity in the relationship of *G. procera* to the mostly Western *G. detonsa* complex. While the chromosome number is said to differ, no published counts of any of its American members are available. For example is *G. procera* an old taxon that evolved in pre-Wisconsin times on the upper Great Plains, as its ecology and morphology suggest, surviving the Pleistocene in small populations on the ice's edge? Or was *G. thermalis*, a common species in the Central Rocky Mountains, or *G. detonsa* to the north, or both, involved in its ancestry? Did the *G. detonsa* (*nesophila*) population of Northern Quebec and Newfoundland play a role in the ancestry of *G. victorinii*?

The great taxonomic-phytogeographic difficulties which the *G. macounii-procera* pheno-cline seems to have engendered, and its relationship to the Gaspé endemics and to *G. crinita*, can thus be resolved by realizing that the two taxa fall into the standard pattern of Eastern North America-Western North America vicarious species pairs with the post-glacially produced modern ranges overlapping in glaciated Northeastern North America. This pattern, or especially that of the western member of each pair, was originally discussed in Fernald's (1925) celebrated "Nunatak Hypothesis," documented as to its prevalence by Hultén (1937), and more recently discussed and documented by many excellent, ecologically and genetically sophisticated papers of Anderson (1936), Wynne-Edwards (1937, 1939), Griggs (1940), Cain (1940), Fassett (1941), Stebbins (1935, 1942), Rousseau (1953), Butters and Abbe (1953), and others. This pattern is much more prevalent than is generally appreciated, and is exemplified by the ranges of many of our commonest as well as rarest species in the Northeastern United States. There are many Western taxa, which, in a general way much like *Gentianopsis*

procera, arrived sometime post-glacially in the Eastern United States, where they were able to invade and survive in ecologically equivalent habitats in a great variety of plant communities (but not necessarily the same as out West!) These include not only the many species listed by Fernald (1925, 1935) and Fassett (1941), or such great Eastern rarities as *Pterospora andromedea*, *Aconitum columbianum* (*A. noveboracense*), *Dodecatheon pulchellum* and *D. amethystinum* (Iltis 1965), or *Illiamna rivularis* (*I. corei*, *I. remota*), but also more common, often locally ubiquitous species, such as *Salix candida*, *S. pyrifolia*, *Potentilla fruticosa* (*P. floribunda*), *P. arguta*, *Geum triflorum*, *Carex flava*, *Schizachne purpurascens*, *Oryzopsis asperifolia*, *Corydalis aurea*, *Valeriana edulis* (incl. *V. ciliata*), *V. sitchensis* (incl. *uliginosa*) (Meyer 1951), *Anemone multifida*, *Geranium bicknellii*, and literally many hundreds more. Most, if not all, of these do not have a closely related sibling in the East.

Of somewhat greater interest are the cases where a pair of species, one of which is Western (Cordilleran, Great Plains, Pacific Northwest, etc.), and the other Eastern (Appalachian, Alleghenian), have been able to migrate far enough from their respective regions of survival to overlap the range of their sibling, *this overlap in almost all cases sharply restricted to the glaciated regions of the Northeastern United States*. With the Western taxon listed first, such vicarious species pairs, in addition to *G. procera* — *G. crinita*, include: *Populus tremuloides* — *P. grandidentata*; *Viola rugulosa* — *V. canadensis* (treated as varieties of *V. canadensis* by Russell 1965); *Viola adunca* — *V. conspersa* (Russell 1965); *Actaea rubra* (incl. *A. arguta*) — *A. alba* (Kane, Iltis, & Kawano, in ms.); *Cynoglossum boreale* — *C. virginianum*; *Cypripedium parviflorum* — *C. pubescens*, and many other species pairs in Orchidaceae; *Juniperus horizontalis* — *J. virginiana* (Fassett 1945); *Senecio pauperculus* — *S. plattensis* (Barkley 1962, 1963, cf. footnote 5, p. 349); *Salix serrissima* — *S. lucida* (Argus 1964) and other species pairs of willows; *Parnassia glauca* — *P. caroliniana* (which relate to each other much like the two *Gentianopsis* species with which they may grow); *Chimaphila umbellata occidentalis* — *C. u. cisatlantica*; *Cinna latifolia* — *C. arundinacea*; *Rhus radicans rydbergii* — *R. radicans radicans*; *Streptopus amplexifolius americanus* — *S. roseus* (Fassett 1935; cf. Löve & Harries 1963); East-West subspecies within *Solidago spathulata* and *S. speciosa* (cf. Cronquist, in Gleason 1962); *Muhlenbergia racemosa* — *M. glomerata*; and many others. The taxa in these pairs may be as distinctive as *Actaea alba* and *A. rubra* or *Streptopus amplexifolius* and *S. roseus*, or as similar as the varieties of *Rubus strigosus* or the species of *Amelanchier*. In many, if not nearly all of the above examples, hybridizations between the two taxa in the region of sympatry has been demonstrated or suspected. The great difficulties that one encounters in distinguishing these poorly differentiated, post-glacially confluent species pairs was well

stated by Hultén (1937) who was among the first moderns to appreciate the dynamics of such a situation: . . . "As long as those races are separated from one another geographically, they may be distinguishable, but when migration has proceeded so far that the radiants from two elementary areas meet, hybridization and thereby an intergradation of the differences must be expected to occur."

The recognition of this large western floristic element in the flora of Northeastern North America is a very important key to the resolution of many taxonomic, phytogeographic, and evolutionary problems in this region, especially in the floristic region of the "White Pine-Hemlock Northern Hardwoods," a region recently glaciated, recently ecologically "open" and receptive, and therefore recently easily invadable. *The restriction of the Western taxa to glaciated lands in their Eastern North American ranges* has far-reaching historical phytogeographic implications, especially regarding the amount of (or lack of) disturbance and vegetational shifting in the Southeastern United States during the Pleistocene. These questions will be discussed in a paper now in preparation. This evidence, however, strongly supports the views of E. Lucy Braun (1950) that the effect of the Pleistocene ice sheet on the Southeastern vegetation was minimal, and that the present ranges south of the glacial maximum of species of the Southeastern forest flora are essentially the same today as they were during the glaciation.

ACKNOWLEDGMENTS

The present study was aided by the University of Wisconsin Research Committee on funds from the Wisconsin Alumni Research Foundation and by travel support from the Botanical Society of America to the Xth International Botanical Congress, where at the Edinburgh Botanical Garden Library Ma's (1951) paper was examined and the first draft written. Publication of illustrations was supported in part by the Norman C. Fassett Memorial Fund. I wish to thank John W. Thomson, Lloyd Shinnars and James Pringle for critical reading of the manuscript and stimulating argument, Mrs. R. Snell for careful work on the manuscript, Drs. J. M. Gillett and J. Rousseau for their kind permission to reproduce illustrations of *Gentianopsis* from their studies, and Dr. John Moore for maps of the Minnesota ranges.

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